BRIEFER ARTICLES.

THE MITOSES IN THE SPORE MOTHER-CELL OF PALLAVICINIA.

(WITH SIX FIGURES)

IN 1894 Farmer published a paper[1] on *Pallavicinia decipiens* reporting the occurrence of very peculiar phenomena in the division of the spore mother-cell. According to his account the nucleus in preparation for division is surrounded by dense protoplasm which projects into each of the four lobes of the mother-cell and forms a four-rayed star. He termed this structure a "quadripolar spindle." After the formation of the "quadripolar spindle," four chromatic droplets make their appearance in the nucleus as the first positive evidence of approaching division. The four chromatic droplets become four chromosomes, which by division are doubled in number. The resulting eight rod-shaped chromosomes point off in pairs towards the four lobes of the spore mother-cell. Further doubling takes place, increasing the total number of chromosomes to sixteen, and four chromosomes pass simultaneously to each pole of the four-rayed spindle, which persists to the end.

Farmer's later studies[2] on other Jungermanniales revealed the presence of the "quadripolar spindle" in the early stages of mitosis, but in no case did he find a repetition of the peculiar conditions described for Pallavicinia. In all other forms the "quadripolar spindle" is a temporary structure, which is later replaced by normal bipolar spindles of two successive mitoses with longer or shorter intervals between. Farmer interprets the temporary four-rayed star of these plants as transitional between the "quadripolar spindle" of Pallavicinia and the normal bipolar spindle.

Davis in 1901 described[3] conditions during spindle formation in the spore mother-cell of *Pellia epiphylla* substantially in agreement

[1] FARMER, Studies in Hepaticae: On *Pallavicinia decipiens* Mitten. Ann. Botany 8:35. 1894.

[2] FARMER, On spore formation and nuclear division in the Hepaticae. Ann. Botany 9:363 and 469. 1895.

[3] DAVIS, Nuclear studies on Pellia. Ann. Botany 15:147. 1901.

with Farmer's studies on the same form, but the two observers differ widely in their interpretation of the facts. Davis considers Farmer's "quadripolar spindle" as a transitory stage of prophase, which should not be regarded as a part of the true spindle that is formed later. The nuclear divisions in the spore mother-cell of Pellia are effected by two successive mitoses, each with a bipolar spindle and the gametophytic number of chromosomes (eight) at the nuclear plate of each metaphase. There is also a well-defined period between the two mitoses when the nuclei are in the resting condition. The events of sporogenesis for Pellia are then essentially the same as those throughout the pteridophytes and in the development of pollen.

The striking peculiarities of Farmer's account of Pallavicinia lie not so much in the presence of a four-rayed achromatic figure as in the reported division of four primary chromosomes into sixteen, and their distribution to form simultaneously four daughter nuclei through the "quadripolar spindle." It is necessary to emphasize this point, since Farmer[4] in a criticism of Davis's paper on Pellia does not consider this matter, while taking exception to Davis's use of the term spindle. Davis found a four-rayed figure during prophase in Pellia, but was not willing to call it a spindle, since the actual distribution of the chromatin takes place in the usual manner at a later period through two successive mitoses, whose spindles are bipolar. The four-rayed structure in Pellia seems to Davis a character of prophase, determined largely by the peculiar crowded condition of the nucleus in the center of a four-lobed cell.

However, Farmer's very positive assertion of the persistence of the four-poled spindle, and his detailed account of the peculiar arrangement of the chromosomes and their simultaneous passage to the four poles in Pallavicinia, makes his position a strong one to assail except upon a reexamination of the conditions in Pallavicinia itself.

I am now at work on *Pallavicinia Lyellii* S. F. Gray, which is abundant in this locality. My studies are by no means complete, but have been carried far enough to justify conclusions on the chief events of sporogenesis, which are presented in this note. I have had the opportunity during past summers at Woods Hole of examining Dr. Davis's preparations of Pellia and have had the benefit of his suggestions and criticisms on technique.

In preparing for mitosis the nucleus of the spore mother-cell

[4] FARMER, The quadripolar spindle in the spore mother-cell of *Pellia epiphylla*. Ann. Botany **15**:431. 1901.

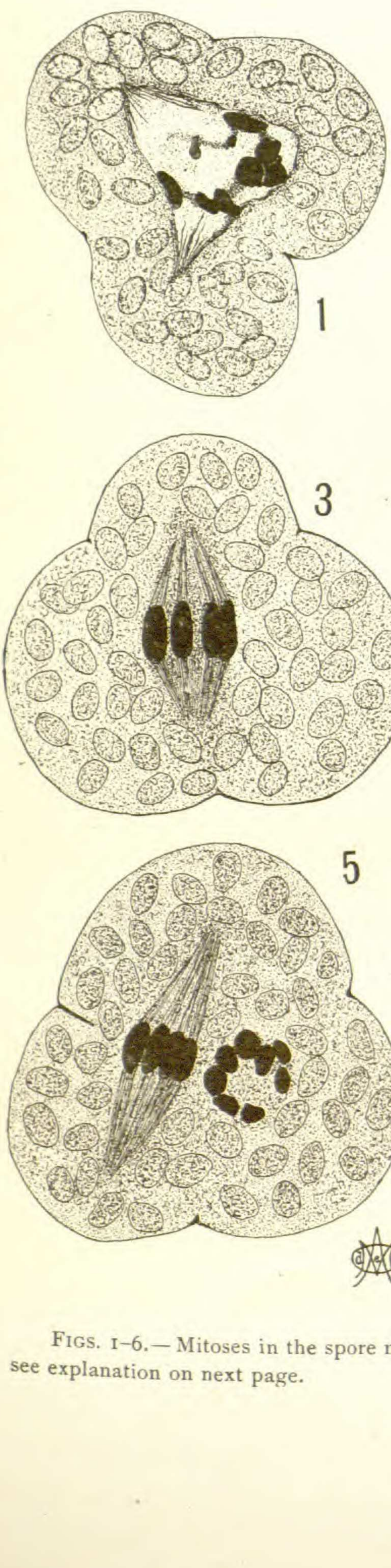
assumes a tetrahedral form, each angle of which points into one of the four lobes of the spore mother-cell. This form persists through synapsis and the spirem condition, and only disappears with the formation of the spindle.

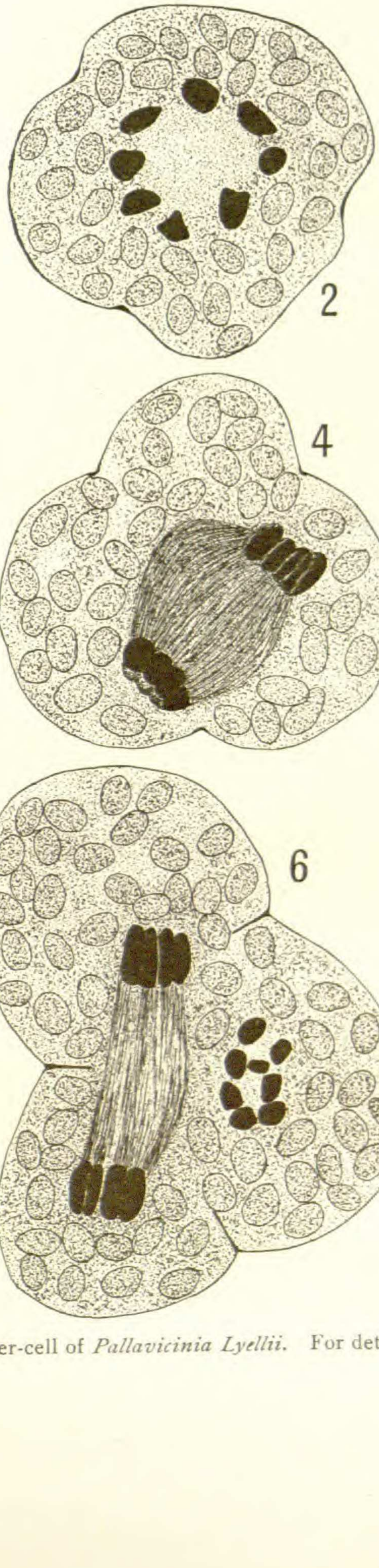
While the chromosomes are being differentiated, and while there is still a trace of linin connecting them, fibers may be seen extending over the points of the tetrahedral nucleus as caps and into the nuclear cavity (*fig. 1*). With the appearance of these fibers the nuclear membrane becomes less distinct, some of the fibers finally occupying the position which it formerly held. During this period the incompletely differentiated chromosomes lie scattered irregularly throughout the interior of the nucleus.

With the complete disappearance of the nuclear membrane and the further growth of the fibers, this four-rayed structure rapidly passes over into a bipolar spindle and the chromosomes, eight in number, become clearly grouped in a ring to form the nuclear plate (*fig. 2*). I have found no evidence of their quadrupling in number, as was so positively asserted by Farmer. It is difficult to follow the development of the bipolar spindle from the four-rayed structure of prophase because the figure is small, but there is probably a rearrangement of the elements through the establishment of a single axis, around which the fibers and chromosomes become grouped.

Now follow two divisions in rapid succession without an intervening resting condition. There is no four-poled spindle in Farmer's sense, but well-organized bipolar spindles without centrospheres, and the chromosomes are distributed in the usual manner. *Fig. 3* illustrates the metaphase of the first division and *fig. 4* shows anaphase of the same. In the latter case the daughter chromosomes are seen to be grouped in a ring at the poles of the spindle. There appears to be no resting period. The second division begins immediately, the rings of chromosomes altering their positions so that their planes lie at right angles. Two distinct spindles are organized, their axes being perpendicular to each other. *Fig. 5* presents the conditions at metaphase of the second division and *fig. 6* illustrates anaphase when the mitoses of the spore mother-cell are completed. It should be noted that the two spindles of the second mitosis are entirely distinct from each other. My preparations show hundreds of examples similar to the stages that I have figured.

It will be seen that the foregoing account agrees substantially with





FIGS. 1–6.— Mitoses in the spore mother-cell of *Pallavicinia Lyellii*. For details see explanation on next page.

that of Davis for *Pellia epiphylla*, with the exception that in Pallavicinia there is no period of rest between the first and second mitoses.

I have carefully followed the nucleus of the spore mother-cell through all stages, from synapsis to the completion of the resting nuclei of the spores, and find that the only structure which could possibly be interpreted as a "quadripolar spindle" is that illustrated in *fig.* 1, which is clearly a condition of prophase. It does suggest Farmer's description of a "quadripolar spindle," and would be so interpreted but for the fact that it is followed by bipolar spindles of the normal type, through which the chromosomes are distributed by two successive mitoses in the usual manner. There is no quadrupling of the primary chromosomes or their simultaneous distribution in four groups to form the four daughter nuclei, which are the most remarkable features of Farmer's account of the activities of a "quadripolar spindle."

The number of chromosomes in *Pallavicinia Lyellii* differs from that reported by Farmer for *Pallavicinia decipiens*. He states that there are four in the gametophyte and eight in the sporophyte. I have not determined the number in the sporophyte, but find eight present in each mitosis in the spore mother-cell. This fact is clearly shown in the accompanying figures.

I hope soon to present a more detailed account of these events of sporogenesis, together with nuclear studies upon other phases in the life history of *Pallavicinia Lyellii*.—ANDREW C. MOORE, *South Carolina College, Columbia.*

EXPLANATION OF FIGURES 1–6.

FIG. 1. Prophase of the first mitosis; the nucleus has a tetrahedral form, the points being directed into the four lobes of the spore mother-cell; fibrillae are gathered at these points but the nuclear membrane has not yet broken down; similar stages of prophase were probably considered by Farmer as quadripolar spindles.

FIG. 2. The eight chromosomes, grouped in a ring at the nuclear plate, are viewed from above.

FIG. 3. Metaphase of the first mitosis; the spindle in all respects a normal bipolar structure without centrospheres.

FIG. 4. Anaphase of the first mitosis.

FIG. 5. Metaphase of the second mitosis; one spindle seen from the side; the other, almost perpendicular to the first, shows the eight chromosomes at the nuclear plate.

FIG. 6. Anaphase of the second mitosis; one spindle seen from the side; the other seen from one end shows a group of eight grand-daughter chromosomes.